bison. After butchering the animal they stored the meat in an underground cellar insulated with grass. The hide was given to their Chief, which he used in their "talking house" as a place to sit. The carcass provided food for their dogs for a long time. Mrs. Titus said this was the last known occurrence of bison in the Tanana area. Recall that Elliot Johnson reports seeing four bison near Fort Yukon, and described how his father-in-law killed a bison in the upper Yukon area, probably in the early 1900s. Mr. Arthur Adams of Beaver said that Jack VanHatten, who with his family lived in the upper Black River area above Grayling Fork during the early 1900s, recounted the story of a trapper who shot a bison in that area. However, the date of this occurrence is unknown. A number of residents of the upper Yukon basin in Alaska provided additional accounts describing tracks or other sign suggesting that a few bison may have occurred in this region as late as the mid 20th century.

The journal of James Geoghegan (James Geoghegan Collection, University of Alaska Archives), who lived near Delta Junction, Alaska in the early 1900s, includes a reference to the presence of bison near Donnelly, Alaska in 1918 or 1920. Unfortunately, it is not possible to determine whether the author is referring to plains bison introduced to this area in 1928 or to the presence of a few indigenous wood bison prior to that time.

Oral Narratives From and About Adjacent Canada

Mr. Moses Sam of Arctic Village said his uncle, Henry John, told him stories about "Indians over Old Crow way" who hunted buffalo for food, although he is not aware of their presence in the upper Chandalar River-Arctic Village area. The late Mr. Isaac Tritt, Sr. of Arctic Village knew that bison occurred in Canada, specifically mentioning the Mayo area in Yukon. However, he was not aware that they occurred in eastern Alaska. He said the *Gwich'in* name for bison was *Dachantèe qwaak'ii*, which he translated as "in the timber, cow."

Mr. Hyacinthe Andre, age 86, and his younger brother Gabe Andre, of Arctic Red River, NT provided information regarding the occurrence of bison in this area (Figure 1). They are most familiar with the lower Mackenzie River area near Arctic Red River. Hyacinthe Andre spent much of his life in the Anderson River country to the east, between the Mackenzie and Horton rivers. The Andre brothers referred to oral traditions describing the former occurrence of bison in this area. Hyacinthe Andre said he had heard "old stories" referring specifically to the Travaillant Lake area east of Arctic Red River as having once supported bison, that bison were once hunted to the north near the arctic coast, and that bison once occurred on the "barren-grounds" adjacent to the Anderson River, mentioning that bison skulls had been found there. He does not recall the *Gwich'in* name for bison, but notes they disappeared a long time ago and that it has been at least 200 hundred years since bison were hunted in the region north of Arctic Red River. Mr. Andre clearly differentiates bison from muskoxen, saying the bison were much larger than muskoxen, and that these animals "were powerful and could run through four feet of snow with no problem."[vii]

Gabe Andre adds that bison also occurred adjacent to the Mackenzie River near Arctic Red River, including the area near the Ontaratue River south of the Mackenzie. He recalls one story that describes how the bison disappeared after a bison head had been sent south to be examined. An account presented by Lotenberg (1996) indicates that bison were hunted near Fort MacPherson, about 30 miles west of Arctic Red River, in the 1820s. These accounts appear to be consistent with the presence of late Holocene bison remains along the arctic coast near Cape Bathurst, on the Old Horton River Channel, and Harowby Bay, about 250 miles northeast of Arctic Red River (Table 1; Figure 3). As described below, one of these specimens is radiocarbon dated at 420±65 years BP.

PALEONTOLOGICAL, RADIOMETRIC, ARCHAEOLOGICAL AND ETHNOGRAPHIC INFORMATION

Paleontological and Radiometric Data

Paleontological discoveries often result from incidental encounters, are influenced by the vagaries of preservation, and in Alaska and Canada often represent isolated rather than mass mortality events (Lyman 1994). Radiometric data for Holocene bison are the product of the chance discovery of specimens and the selection of samples for dating by various investigators during the last few decades. The oral narratives presented above reflect the accumulated knowledge of people whose accounts are chronologically ordered, but sometimes do not contain precise temporal referents.

Table 1 presents available radiometric data for bison remains collected in Alaska and northwestern Canada that are dated to either late in the Pleistocene-Holocene transition (Guthrie 1995) or to the Holocene. Except for specimens dated by the sedimentary matrix within which they were found (Nos. 4, 9, 17, 18, 23, 25, 26, and 41), dates for Holocene bison are derived directly from bone. The sample of dated specimens includes some from known geological and sedimentary contexts, others found in direct association with archaeological and cultural material, and some without established associations.

The sample of Holocene bison includes 47 dated specimens from 44 locations, including 19 specimens from Alaska and 28 from Canada (Table 1, Map Nos. 1-44). Conventional radiocarbon ages provided by the laboratory conducting each assay, or as reported in published literature are listed in Table 1. Males (n=15) predominate over females (n=4) in the sample of Holocene remains of known sex (Table 1), probably because the remains of male bison are more robust and will tend to persist longer than the remains of females. The ten earliest radiocarbon dates listed in Table 1 represent temporally late, eastern Beringian representatives of the Mammoth-Steppe Fauna, a widespread faunal community associated with steppe-tundra and found throughout Beringia (Guthrie 1982,1985, 1990; Matthews 1982; Vereschagin and Barynishnikov 1982; Burke and Cinq-Mars 1998).

MAP NO.	LOCATION	CONVENTIONAL 14C AGE	REFERENCE	LAB NO.	COMMENTS
-	Old Crow, (Loc. 11-1) Y.T.	11,990±180	Harington 1978	I-7765	Bison scapula
-	Fairbanks Creek, AK	11,980±135	Harington 1978	ST-1633	Bison bone
-	Birch Creek, Yukon Flats, AK	11,900±70	ADF&G, this study	Beta-67494	Female bison skull with horn sheaths
-	Cleary Creek, AK	11,735±130	Péwé 1975	ST-1631	Bison bone
-	Old Crow Flats, Y.T.	11,530±200	Harington 1977	QU-780	Bison humerus
-	Broken Mammoth Site, Delta Junction, AK Cultural Zone IV	11,510±120 11,420±70	Holmes 1996	WSU-4262 CAMS 5358	Bison bones with processing marks; associated hearth charcoal dates
-	Dry Creek, AK	10,715±225	Guthrie 1985	ST-1561	Bison bone
-	Lost Chicken Creek, AK	10,370±160	Harington 1978	I-8582	Distal portion of bison tibia
-	Broken Mammoth Site, Delta Junction, AK Cultural Zone III	10,290±70 10,270±110	Holmes 1996	CAMS-5357 WSU-4263	Bison bones with processing marks; associated hearth charcoal dates
-	Bluefish Cave II (MgVo-2) Y.T.	10,230±140	Burke & Cinq-Mars 1998	RIDDLE-561	Bison metacarpal at archaeological site
1	Engigstciak, Y.T.	9870±180 9770±180 9400±230	Cinq-Mars et al. 1991	RIDDL-362 RIDDL-281 RIDDL-319	Bison bone (tibia, metacarpal, and metatarsal) showing processing marks
2	Muskeg River, N.T.	9645±190	Harington, this study	I-9997	Bison cranial fragment
3	Cape Bathurst, N.T.	9560±60	Harington, this study	Beta-79861 CAMS-18424	Left bison scapula
4	Gerstle River Quarry Site, AK	9970±60 8280±60	Holmes 1998	Beta-98432 Beta-98434	Bracketing dates from charcoal for 6 bison bones
5	Porcupine River, AK	9000±250	UAF Museum, unpublished	Beta-18552	Bison bone
6	Victoria Island, Minto Inlet, Kuujjua River, N.T.	8080±60	Harington, this study	TO-3709	Partial male *B. bison* skeleton with cranium and horn cores
7	Broken Mammoth Site, Delta Junction, AK. Cultural Zone II	7600±140	Holmes 1996	WSU-4264	Bison bones with processing marks; associated hearth charcoal date
	Cultural Zone IA	2260±40	D. Yesner, pers. comm.	Beta-128716	Bison naviculo-cuboid; associated charcoal date
8	Mt. Granger, Whitehorse, Y.T.	7510±90	M. Hoefs, pers. comm.	Beta-135361	Female *B. bison* horn sheath from alpine ice patch
9	Canyon Site, Aishihik River, Y.T.	7195±100	Workman 1978 Harington 1978	SI-1117	Bison bone fragments around buried hearth; associated charcoal dates
10	Sullivan Pit, AK	6730±260	Repenning et al. 1964	W-1108	Bison bone
11	McIntyre Creek, Y.T.	ca 5840±70	Hare, this study	Beta-70100 CAMS-11243	Bison bone associated with cultural material
12	Goldstream Creek, AK	5340±110	Péwé 1975	SI-845	Bison horn sheath
13	Harrowby Bay, Beaufort Coast, N.T.	5230±110	Cinq-Mars 1991 Harington 1990	RIDDL-321	Metacarpal at archaeological site
14	Fort Yukon, AK	5045±45	Guthrie, this study	AA4379 VP4157	Male *B. bison* skull
15	Carmacks, Y.T.	4880±80	Harington, this study	Beta-25120	*B. bison* skull from terrace
16	Julian Site (JcRw-13) Fisherman Lake, N.T.	4800±160	Morlan 1999	S-0906	Bison bone at archaeological site
17	Canyon Site (JfVg-1) Y.T.	4730±320	MacNeish 1964	W-1125	Bison bone; associated charcoal date
18	Kusawa Bluffs Site (JdVa-2), Y.T.	4490±130	Greer 1986	Beta-14402	Date from elk bone located below bison bones in archaeological site
19	Black River, Yukon Flats, AK	4495±60	ADF&G, this study	Beta-65662	Male *B. bison* horn core and cranium
20	Black River, Yukon Flats, AK	4390±70	ADF&G, this study	Beta-136731	Male *B. bison* skull with horn sheaths
21	Fort Yukon, AK	3710±70	ADF&G	Beta-74344	Female *B. bison* horn core and part of cranium
22	Fort Yukon, AK	3520±40	Gerlach, this study	Beta-104823	Male *B. bison* skull with both horn sheaths
23	Delta River Overlook Site (XMH-297), Delta Jct., AK	3980±150 2285±145	Holmes and Bacon 1982	GX-6752 GX-6750	Bison tibia fragment; associated charcoal dates
24	Ruby Range, Kluane District, Y.T.	3470±70	M.Hoefs, pers. comm.	Beta-136362	Bison tibia at archaeological site
25	Pelly Farms Site (KfVd-2) Y.T.	3160±70	MacNeish 1964	S-193	*B. bison*; associated charcoal date
26	Pelly Farm Site (KfVD-2) Y.T.	2920±140	MacNeish 1964	GSC-127	*B. bison*; associated charcoal date
27	Fairbanks, AK (railroad terminal)	2900±80	Guthrie, this study	AA3320, AMNH A-501-5331	Male *B. bison* skull
28	Montague House, Y.T.	2800±60	Hare, this study	Beta-70101	Bison ribs

MAP NO.	LOCATION	CONVENTIONAL 14C AGE	REFERENCE	LAB NO.	COMMENTS
29	¾ mile downstream from Circle, Yukon Flats, AK	2545±80	Guthrie, this study	AA3217, AMNH A-479-4783	Male *B. bison* skull
30	Lower Tanana River, AK	2460±70	Guthrie, this study	unknown	Male *B. bison* skull
31	Braeburn, Y.T.	2460±40	M.Hoefs, pers. comm.	Beta-137731	*B. bison* skeleton in dry lake bed
32	Killik River (Site KIR 275), AK	2330±50	C. Martin, T. Birkedal, pers. comm.	Beta-130571	Bison metatarsal near archaeological site
33	Kluane Lake, (Congdon Creek) Y.T.	2180±30	M.Hoefs, pers. comm.	Beta-91755	Male *B. bison* cranium
34	Takhini River, Y.T.	2150±40	M. Hoefs, pers comm.	Beta-91756	Male *B. bison* frontal
35	Finlayson River, Y.T.	2200±60	Harington, this study	Beta-79854	Young male *B. bison* cranium
36	Baillie Islands, N.T.	1890±90	Harington 1980	I-5407	Bison horn sheath
37	Black River, Yukon Flats, AK	1730±60	ADF&G, this study	Beta-62999	Male *B. bison* skeleton
38	Dawson (Loc. 16), Y.T.	1565±85	Harington, this study	I-11051	Bison tibia, apparently fractured by humans
39	Quartz Creek, Dawson, Y.T.	1430±95	Harington 1977	I-5405	*B. bison* horn core
40	Tetlin-Tanacross area, AK	1270±55	Guthrie, this study	AA3218, AMNH A-393-1013	Male *B. bison* skull
41	Frenchman Lake Site (KaTx-6), Y.T.	<1250	J. Hunston, pers. comm.		Bison bone above White River Ash
42	Cowley Lake, Y.T.	940±90	Harington, this study	Beta-69762	Female *B. bison* skull
43	Old Horton River mouth, N.T.	420±65	Harington 1990 Morrison 1997	Beta-28765	Small adult male *B. bisons* skull showing cut marks
44	Anchorage, AK	170±30	Gerlach, this study	Beta 136732	Male *B. bison* skull with horn sheath

Table 1. Location and radiocarbon dates for bison specimens representing the end of the Pleistocene-Holocene transition or the Holocene in Alaska and adjacent Canada. Map numbers for specimen dates within the last 10,000 years correspond to those in Figure 3. Most radiocarbon ages are corrected for isotopic fractionation.

Several dated and undated specimens of northern small horned bison have been taxonomically referred to *B.b. athabascae* (cf. Skinner and Kaisen 1947; Harington 1977; van Zyll de Jong 1986). Measurements from these and other Holocene specimens for which cranial and postcranial material are sufficiently intact to allow morphometric analysis (specimens designated as *B. bison* in Table 1) indicate they are appropriately regarded as *B.b. athabascae*. This conclusion is based on comparisons with morphological data published by van Zyll de Jong (1986). The temporal and geographic distribution of these remains (Table 1, Figure 3) is consistent with earlier conclusions regarding the widespread occurrence of relatively small-horned bison, representing *B.b. athabascae*, in Alaska and northern Canada during the mid and late Holocene.

Radiometric data for a large number of Pleistocene and some Holocene bison have been previously published by Guthrie (1990), Harington (1977, 1978, 1980a, 1980b, 1989, and 1990) and others. The geographic location of dated Holocene specimens, and four undated specimens of small-horned bison, is shown in Figure 3. The distribution of wood bison during the mid and late Holocene as indicated by currently available radiometric data is also shown, as is the region in Alaska and northwestern Canada where oral and/or written accounts describe the presence of bison during this period (van Zyll de Jong 1986; Gates et al. 1992; Lotenberg 1996; this study).

The temporal distribution of available radiocarbon dates representing Pleistocene and Holocene bison in Alaska and adjacent Canada, based on data compiled in this study and by Guthrie (1990), C.R. Harington (radiocarbon table in Annotated Bibliography of Quaternary Vertebrates in Northern North America) and others, is shown in Figure 4. These data are the cumulative result of a variety of paleontological and archaeological studies over many years. While this sample reflects some degree of randomness, the compilation also reflects an early emphasis on dating relatively large horned Pleistocene bison, as well as a more recent emphasis on dating small horned Holocene specimens and bison remains found in archaeological contexts. Additional late Pleistocene dates were recently obtained from bison remains found on Alaska's North Slope (Matheus et al. 1999), but are not represented in Figure 4.

Radiometric and zooarchaeological data demonstrate that bison occurred in this region during the late Pleistocene and Holocene, and that the late Holocene distribution of wood bison included much of eastern Alaska, southern Yukon, the western NT, and possibly western Alaska as well (Skinner and Kaisen 1947). Well preserved bones indicate their presence along the arctic coast of the Yukon and NT, and on Victoria Island (Figure 3); oral accounts, as well as the archaeological evidence reviewed below (Morrison 1997), indicate the distribution of wood bison overlapped to some extent with that of muskoxen and caribou in parts of this region. Radiometric evidence discussed below also indicates that bison occurred near the arctic coast of Canada and in the northern Brooks Range in Alaska during the late Holocene.

Radiocarbon data indicate that bison occurred in Alaska at least as recently as 170±30 BP, based on a skull found at Anchorage (Map No. 44).[viii] Although there are currently no historic accounts regarding the presence of bison south of the Alaska Range, this specimen indicates they were present in

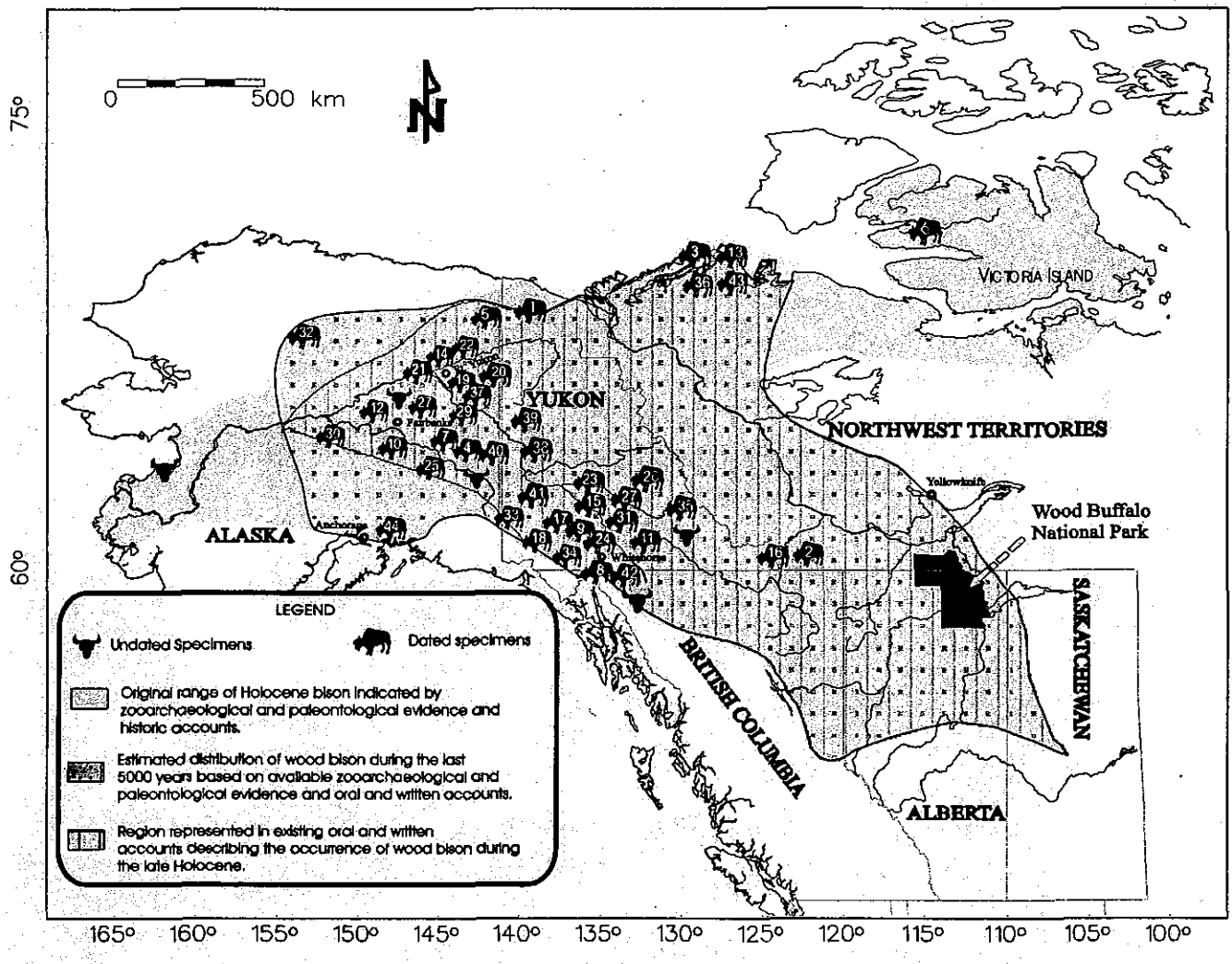

Figure 3. Approximate location of Holocene bison remains in Alaska and adjacent Canada, and estimated original and late Holocene range of wood bison in North American based on available zooarchaeological, paleontological, oral and written historical documentation (Skinner and Kaisen 1947; McClellan 1975, 1981; van Zyll de Jong 1986; Gates et al. 1992; Lotenberg 1996; this study). Location numbers correspond to map numbers in Table 1.

this area during the late Holocene. The lower Matanuska and Susitna river drainages near Anchorage contain extensive meadows that may have supported bison populations in the past. Radiocarbon dates for specimens collected in the upper Yukon and Tanana river lowlands, as well as oral accounts, indicate that bison also inhabited those areas during the late Holocene, further suggesting that low-elevation meadows were a component of wood bison habitat in Alaska.

Bison remains are distributed geographically from west to east across Alaska and into Canada (Figure 3), and temporally throughout the Holocene (Figure 4). The area represented by oral narratives encompasses the area where late Holocene bison remains appear to be most common. The available chronometric data and historic accounts suggest that wood bison were more common in eastern Alaska and the southern Yukon during the late Holocene than in areas to the north and west. However, the two specimens yielding the most recent radiometric dates occur some distance outside (Anchorage), or near the edge (arctic coast, Northwest Territories) of the area referred to in the oral accounts, indicating that wood bison persisted into the last millennia over a broader area than is indicated by currently available historical accounts. The area south of the Alaska Range in Alaska is the only extensive region where physical evidence for late Holocene bison is not presently corroborated by oral and/or written historical documentation (Figure 3).

ARCHAEOLOGY

Alaska

Archaeological investigations in interior Alaska are limited, consisting largely of site surveys (e.g., Dixon et al. 1985; Libby and Medlock 1979; Roseneau et al. 1975) with limited systematic excavation. Alaskan archaeological sites at which bison remains have been positively identified include the Dry Creek site near Healy (Powers et al. 1983), the Broken Mammoth (Holmes 1996), XMH-297 (Holmes 1979; Holmes and Bacon 1982) and Gerstle River (Holmes 1998) sites near Delta Junction, and the KIR-275 site in the north-central Brooks Range.

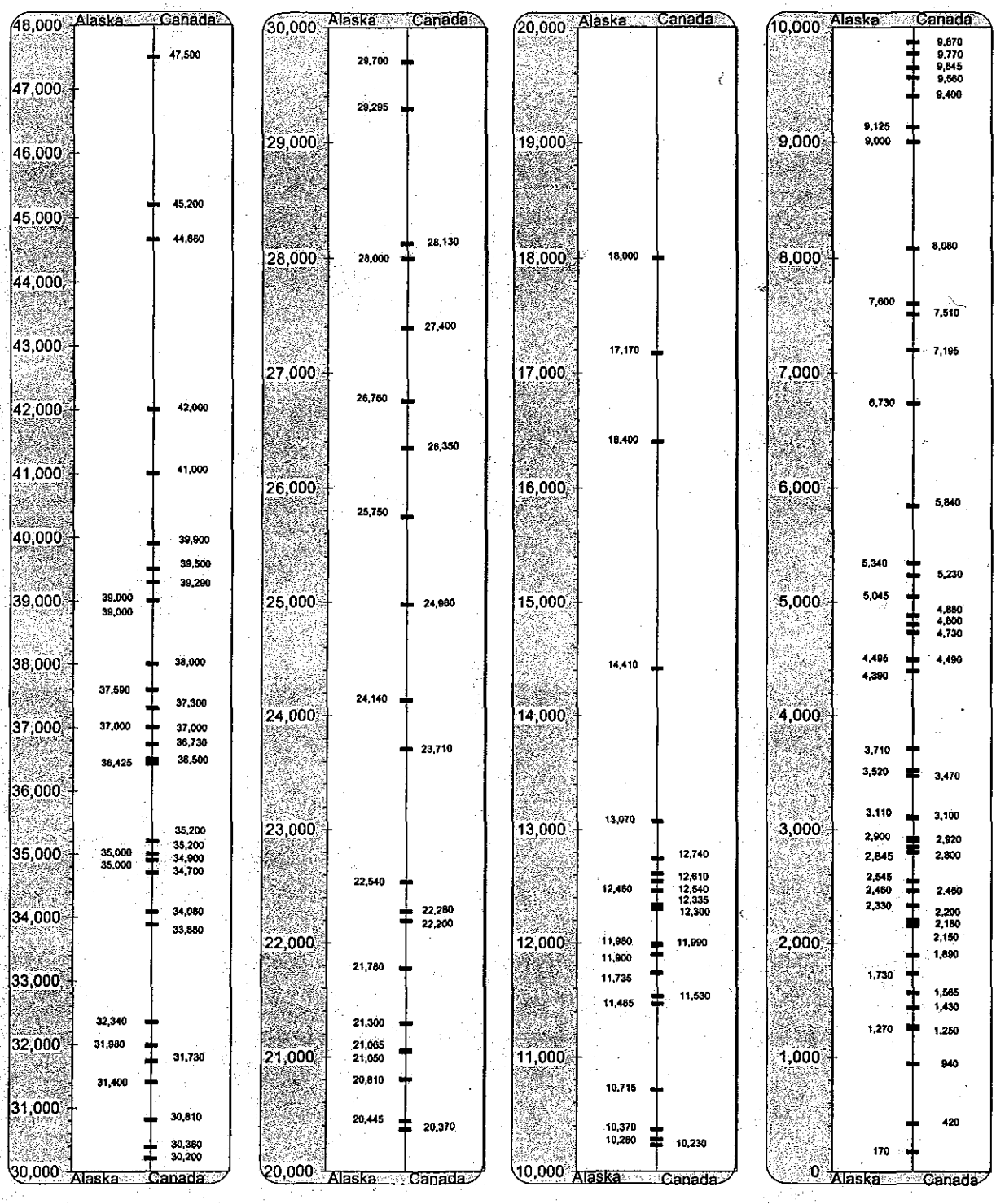

Figure 4. Temporal distribution of uncalibrated radiocarbon dates (years before present) for late Pleistocene and Holocene bison in Alaska and adjacent Canada. The median date was used in two cases where bracketing dates were available for Holocene bison. Dates later than 12,000 B.P. are detailed in Table 1. Pleistocene dates are based on published and unpublished data from Larsen (1968); McDonald (1981); Guthrie (1990); Bureau of Land Management, Fairbanks, open files; S. Dickson (pers. comm.); and the Annotated Bibliography of Quaternary Vertebrates of Northern North America, C.R. Harington, manuscript.

The Broken Mammoth site yielded a variety of bison bones in four "cultural zones." Five radiocarbon dates for bison remains range from 7600±140 to 11,420±70 BP, and a sixth bison bone was recently dated stratigraphically at 2260±40 BP (D. Yesner, pers. comm.). Part of a bison tibia found at the XMH-297 site was stratigraphically dated to between 2285±145 BP and approximately 3980±150 BP, shortly after the fall of the Jarvis Ash (Holmes and Bacon 1982). Bison remains at the Gerstle River site include a phalanx, metatarsal, naviculo-cuboid, calcaneum, and fragments of a

scapula and sacrum in strata bracketed by charcoal dates of 8280±60 to 9970±60 BP (Holmes 1998). A bison metatarsal found near the KIR-275 archaeological site in the Killik River drainage has been dated at 2330±50 BP (C. Martin and T. Birkedal, pers comm.). The late Holocene date was subsequently corroborated by dates of 2470±50 and 2500±50 BP (P. Matheus, pers comm.). Isolated bison remains have also been found in late Holocene flood-plain deposits in interior Alaskan streams, but most are not dated or are from ambiguous stratigraphic contexts (Péwé 1975a, 1975b).

Yukon and Northwest Territories

Archaeological surveys and excavations conducted in northwest Canada, primarily in Yukon, provide additional insight into the occurrence of bison during the Holocene. Radiocarbon dates for bison remains spanning much of the past 10,000 years have been obtained from a number of archaeological sites, including those in Table 1 (Map Nos. 1, 9, 11, 13, 16, 17, 18, 24, 25, 41 and 43). The Engigstciak site in northern Yukon represents the earliest known association of bison remains with cultural artifacts in this region (Cinq-Mars et al. 1991). The majority of dates in the sample of Holocene sites occur between about 3,000 and 6,000 years BP. The only archaeological site with bison remains dated to within the past 1,200 years is the Bison Skull site (OaRw-2). In 1987 a bison skull with attached horn cores was discovered at this site, located along the banks of the Old Horton River Channel (Le Blanc 1988), near the extreme northwestern arctic coast of the Northwest Territories (Map No. 43, Table 1). The specimen yields a radiocarbon date of 420±65 BP (Harington 1990). The skull was found in close association with the skulls of two muskoxen at a site that had a long history of human use, primarily for caribou hunting and butchering (Le Blanc 1991; Morrison 1997). Cut marks on the upper surface of the bison skull suggest it was used as a cutting platform.

Late Holocene sites in the Old Crow area include two extensive spring caribou hunting sites: Klo-kut MjVl-1 (Morlan 1973) and Rat Indian Creek MjVg-1 (Le Blanc 1984). Both sites contained large, well-preserved faunal assemblages with abundant caribou remains and a diverse array of other species, including moose. No bison bones were reported at these sites. Other large-scale excavations include the Old Chief site MjVk-7 (Cinq-Mars 1974; Donahue 1974), NbVk-1 (Morlan 1972a), Cadzow Lake (Morlan 1972b) and the Whirl Lake site MjTp-1 located near the MacKenzie River Delta (Gordon and Savage 1973, 1974). These sites range from mid-to-late Holocene in age and several contain extensive faunal assemblages. The late Holocene component at the Whirl Lake site (dating to uncalibrated AD 1740±90 and AD 1730±90) contained remains of caribou and moose, 15 elements from an unidentified artiodactyl and 17 unidentified large-sized mammal bones (Gordon and Savage 1974). Gordon and Savage (1973) discuss the possibility that bison are represented at this site, although the reasons for this suggestion are not explicit.

Cultural practices and/or poor preservation may obscure the significance of bison as a food resource during the last millennium, at least in southern Yukon. Bone preservation appears to be less problematic at certain sites in northern Yukon where permafrost and rapid soil deposition improve preservation. Faunal remains of large mammals such as moose and bison are well represented at various mid-Holocene sites in southern Yukon (cf. MacNeish 1964; Workman 1978), but there appears to be a paucity of identifiable large mammal bones at late Holocene sites.

Greer (*in prep*) examined faunal assemblages from late Holocene components at 38 archaeological sites in southern Yukon, representing the past 1200 years. These include more than 125,000 bone fragments, most of which could not be specifically identified. The large mammal component is determined for only 16 bones or bone fragments. Caribou occurred with the highest frequency, followed by Dall sheep (*Ovis dalli*). Moose were identified at only one site (JcUj-12), and no bison remains were identified. Greer (ibid.) indicates that several unidentified bone samples were large enough to represent moose, although the possibility exists that some may represent bison.

The intensive processing of large mammal bones during the late Holocene may also be related to changes in cooking and preparation techniques. Late Holocene archaeological sites in southern and central Yukon are characterized by an increase in the occurrence of fire-cracked rock, which Charlie and Clark (1993) indicate may be related to the increased use of stone boiling techniques (Clark and Gotthardt 1997). Intensive processing of large mammal bones to produce bone grease is well documented in the ethnographic record (cf. Leechman 1954; Binford 1978, 1981). Greer (*in prep*) suggests large mammal bones were smashed into small fragments to facilitate the extraction of bone grease, often making it difficult or impossible to determine the species represented at late Holocene sites. Other cultural practices can further complicate the interpretation of faunal remains at archaeological sites, including the practice of disposing of the bones of some species in rivers, lakes or in fires, placing remains in trees and using bones to manufacture tools (McClellan 1975; O'Brien 1997).

Paleontological, archaeological (Table 1) and ethnographic evidence (Lotenberg 1996) shows that bison occurred in Yukon and were harvested by First Nation hunters during the late Holocene, although bison are not highly visible in the archaeological record. The same appears to be true for moose, which, on the basis of Greer's sample, are nearly invisible in the late Holocene archaeological record. The relatively large size of bison and moose probably increases the probability that carcasses were processed extensively at kill sites, further reducing the likelihood that largely intact bones would accumulate at archaeological sites (Binford 1978, 1981, 1983). The fact that high-ranked resources (Smith 1983; Simms 1984; Smith and Winterholder 1992; Broughton 1997; Janetski 1997) such as moose and bison are most susceptible to overexploitation could also account for the low frequency of their remains in archaeological sites (Broughton 1997; Kay 1994a, 1994b, 1997).

ETHNOHISTORY AND ETHNOGRAPHY

There are numerous ethnohistorical studies describing *Gwich'in* Athabascan lifestyles during the early contact period (Franklin 1970, 1971; Dall 1898; Hardisty 1872; Jones 1872; Kirkby 1865; Mackenzie 1801; Murray 1910; Petitot 1970; Richardson 1851, Vol 2; Whymper 1868), but these accounts include no mention of bison. The same is true of ethnohistorical research into the *Gwich'in* fur trade era during the mid- to late-nineteenth century (Krech 1976, 1978, 1979, 1981, 1987), focused loosely as it is on historical context, economics and the response of Native societies to Euroamerican influence. Although written records place bison in southern Yukon and the western NT during and after the mid 1700s (Gates et al. 1992; Lotenberg 1996), we have yet to find written documents placing bison in Alaska at the same time. Similarly, traditional knowledge regarding the late Holocene occurrence of bison in the upper Porcupine-Peel River area is not reflected in the journals of Archdeacon Robert McDonald (Archives of the Ecclesiastical Province of Rupert's Land, Winnipeg), who traveled in the region from 1862 until the early 1900s, or in other written accounts from the region (R. Le Blanc, pers. comm.).

Formal ethnographic studies in northeastern Alaska began in the early 1930s when Osgood (1936) studied the Peel River and Crow Flats *Gwich'in*, and McKennan (1965) began systematic studies with the Chandalar *Gwich'in*. Subsequent research includes studies by Balikci (1963a, 1963b), West (1963), Leechman (1954) and Slobodin (1962, 1981). Except for one intriguing clue, these studies contain no specific references to bison procurement or use.

McKennan (1965:18) notes: "Muskoxen, now extinct in the area, were said to have frequented the Chandalar territory in former days, and a small mountain near the forks of Smoke Creek [Figure 1] is known to the natives as [*ch'itthay ik*; James Kari pers. comm.) which they translate as Muskox Shirt Mountain." However, McKennan's original field notes, and information supplied by *Gwich'in* elder Moses Cruikshank and by Thomas E. Taylor, suggest McKennan may have been provided with a name reflecting the occurrence of "buffalo," but later concluded his informants were referring to muskoxen.

McKennan's original field notes,[ix] reflecting information obtained in 1933, primarily from Chief Christian, read as follows:

Musk Ox [*ch'itthay*]
[*ch'itthay ik*] = Buffalo (sic) shirt.
Little Mt. on Smoke Creek.
Musk ox formerly driven
over cliff on top.

McKennan apparently assumed the informant's reference to "Buffalo" was incorrect (as indicated by his insertion of "sic"), whereupon he changed it to "Musk ox."[x] Moses Cruikshank indicates that a mountain known as "Buffalo Shirt Mountain" was located in the "Sheenjek River country," in the next large drainage east of the Chandalar River. This geographic discrepancy may simply reflect Mr. Cruikshank's reference to a general geographic region in the foothills of the Brooks Range. United States Geological Survey (USGS) topographic maps identify a mountain between the lower reaches of Smoke Creek and the Wind River as "Buffalo Mountain" (Figure 1), based on information provided to USGS engineer T. E. Taylor by local residents (Orth 1971).[xi] His records, as cited by Orth (1971), indicate the name "Buffalo Mountain" was provided to him by residents of Venetie when he visited that community in November 1956. Taylor reviewed local place names with Venetie elders, using aerial photographs and 1:250,000 quadrangles to identify topographic features and inquire as to their names. Mr. Taylor recorded phonetic spellings of *Gwich'in* place names in notes and on maps. Many *Gwich'in* also spoke English and provided English equivalents for place names, as shown on current USGS topographic maps.

Venetie elders informed Taylor that the English name for the mountain was "Buffalo Shirt," and that the name arose from stories indicating that "buffalo" were formerly hunted there. Oral tradition described how buffalo were driven over an escarpment at this site. Taylor's informants stated this animal no longer occurred in the region and that they themselves had not seen or hunted buffalo. They did not speculate regarding the reasons for their disappearance, but were resigned to the fact that the buffalo were gone. Taylor said his informants stated "emphatically" that these animals were "buffalo," and were aware of the difference between bison and muskoxen. He indicates further that he did not question these statements, in part because there seemed to be no doubt as to their meaning, and because he was aware of the existence of wood bison in Canada.

The fact that a few muskoxen apparently persisted in the eastern Brooks Range until the late 1800s makes it difficult to clarify the ambiguity reflected in McKennan's field notes. Lent (1998) reviews historical data regarding the presence of tundra muskoxen in Alaska, and notes there is no subfossil evidence of Holocene muskoxen in the eastern Brooks Range. Oral and written accounts cited by Lent show that small numbers were present in this area in the late 1800s, and that several muskoxen were killed in the upper reaches of the Sheenjek and Chandalar drainages on at least two occasions in the 1890s. However, knowledge of group sizes characteristic of muskoxen and wood bison (Tener 1965; Komers et al 1993), as well as the apparent scarcity of muskoxen in the area, suggest that a herd of the size implied in oral accounts about "Buffalo Shirt Mountain" would be more typical of bison.

DISCUSSION

Zooarchaeological, paleontological, oral and written historical data demonstrate that wood bison populations persisted in a large part of their original range in Alaska and Canada during the late Holocene, and were a component in the economies of Athabascan people in central and eastern Alaska during this period. Their corresponding significance in adjacent parts of Yukon and NT is also indicated. The zooarchaeological record and oral accounts from a wide

geographic area indicate that wood bison occurred on more than a sporadic basis in the late Holocene, and were sufficiently abundant to persist for a period of several thousand years. Oral narratives from Athabascan elders in Alaska and Yukon indicate bison were procured on more than an occasional or intermittent basis, with some historic accounts emphasizing the importance of bison as a resource. Although multiple oral accounts indicate that bison were indeed a source of food and materials, the precise nature of their seasonal, annual, and long term significance relative to other plant and animal resources is unspecified.

Extensive paleontological and limited archaeological data, in combination with oral accounts, indicate that wood bison were hunted by humans until their disappearance from Alaska during the last few hundred years. Wood bison had apparently become scarce shortly before early Euroamerican explorers, naturalists, and entrepreneurs entered Alaska from the east, and before firearms became widely available (Jennings 1968, Holmes and Bacon 1982, Guthrie 1990). In terms of historical context this decline coincided with the period during which bison were largely extirpated from the woodlands east of the Mississippi River (Dary 1989; Belue 1996), the period between the landing of the Mayflower in 1620 and the Lewis and Clark Expedition in 1804-1806, and with the Russian exploration of Alaska's western coast (Bancroft 1886). Wood bison disappeared from substantial portions of their original range in Alaska and Canada by the early 19th century.

Lotenberg (1996) reevaluated the history of wood bison in Yukon primarily on basis of traditional knowledge obtained through interviews with Native elders representing six First Nations in Yukon and northern British Columbia, as well as from previously published records. These accounts indicate wood bison were relatively abundant in a large portion of this region approximately 400 years ago, and continued to inhabit parts of southern Yukon during most of the last 400 years. Based on reports from Native elders, McClellan (1975) concluded that bison populations were declining in parts of Yukon during the eighteenth century, and that Inland Tlingit shot bison with arrows, although their importance in the subsistence economy was not addressed (McClellan 1981). Other traditional stories from southern Yukon also mention the former presence of bison (Sidney et al. 1977). The occurrence of bison in Yukon during the 1800s and early 1900s is corroborated by a limited number of documentary records (Clarke 1945; Jeckell 1933; Gates et al. 1992). The reported occurrence of bison near the Canadian border at Eagle, near Circle, and near Fort Yukon, Alaska, and two reports of bison being killed in interior Alaska during the early 1900s (this study), further suggest that wood bison persisted into the 1900s in Yukon, and that small numbers of bison also occurred, at least on a transient basis, in eastern Alaska adjacent to the Canadian border during this period.

Oral accounts detailed above indicate substantial bison populations were present in Alaska as recently as 200 years ago. Radiometric data corroborate their presence during the late Holocene, with one radiocarbon date indicating bison were still present in Alaska during the early 19th century, although in an area where there are no known historic accounts. The likelihood of finding and dating remains of the most recent wood bison is influenced by many factors, including the rate and duration of population decline prior to the disappearance of the species. Considering the improbability of finding or obtaining samples from the last wood bison in Alaska, the temporal gap between oral accounts and radiometric data in interior Alaska and southern Yukon is not unexpected.

The ability of humans to observe environmental phenomena, and to record and transmit historical knowledge, provides more comprehensive insight into the recent past than can be obtained from zooarchaeological data alone. This is especially true for phenomena that are difficult or impossible to reconstruct through paleontological or other proxies.

A substantial but not exhaustive search for written documents has been completed. The apparent absence of written documents referring to bison in Alaska may indicate that bison had become scarce by the early 1800s, before there was a significant Euroamerican presence in eastern Alaska. Although small numbers apparently persisted until the early 1900s, the handful of early travelers who produced journals or other written records may have remained unaware of, or failed to record, their presence. That early 20th century ethnographers failed to collect information about bison hunting in the north may reflect the limitations of a restrictive working paradigm that focused largely on the contemporary landscape, as well as a sometimes limited sample of informants (Osgood 1936; McKennan 1965; Burch and Mishler 1995). Knowledge of Alaska's faunal history was comparatively limited when the early ethnographic studies were undertaken, with little or no published information indicating that bison might have persisted into the late Holocene. Information about an animal that was no longer present may not have been elicited nor, in the absence of a direct question, offered. Alternatively, as often occurs with other early records, pertinent information may have been available but was simply not included in written accounts (Lyman 1998).

There are similarities in the oral narratives provided by Yukon (Lotenberg 1996) and Alaska Native elders, as well as some elements that are found only in one or the other oral tradition. The diverse content of these accounts is typical of the varying nature of detail encountered in oral narratives passed from one generation to another, representing events and observations occurring from one to several generations earlier. Similarities include: (1) descriptions of the presence of substantial bison populations at one time; (2) indications that bison were hunted extensively, were a major source of food, and provided raw material for clothing and other uses prior to their decline and disappearance during the last few hundred years; (3) indications that late Holocene bison populations were found primarily in low elevation habitats; (4) reports that bison skulls and other remains continue to be found in areas historically known as bison range; (5) observations that moose were absent or scarce at the time bison were abundant; (6) consistent narratives indicating that bison were hunted with bow and arrow; (7) indications that trees and shrubs expanded during and after the period when

bison declined and disappeared, and moose populations expanded; and (8) that several elders from different areas remembered traditional names for bison.

Information found only in Yukon accounts includes descriptions of the use of snares to take bison, and the use of bison horn to make spoons. One account describes the yellow fat that is peculiar to bison, and a few elders indicated that their parents or grandparents hunted bison (Lotenberg 1996). Information peculiar to the Alaskan accounts includes: 1) observations that meat was dried for winter use; 2) that there may have been two types of bison; 3) that hides were used for blankets and pillows and hair was used as thread; 4) that the animal had a long tail and a large hump and head; 5) a reference to the non-allergenic nature of bison hides; 6) indications that bison and moose contributed jointly to the Athabascan subsistence economy at one time; and 7) that dogs were used to hunt bison. There are also indications that drives were used to kill bison in the mountains north of the Yukon Flats in Alaska. However, other accounts mention that drives may have been used to take muskoxen in the upper Chandalar drainage and in the upper Porcupine River region in Canada. The degree to which drives were used to procure bison and/or muskoxen remains unclear.

Accounts from both Alaska and Yukon include a few observations of bison or their sign indicating that small numbers of bison occurred, at least on a transient basis, after the decline of larger and geographically more widespread populations. Both sets of accounts include a few possible reasons for the decline or disappearance of bison populations. Yukon elders mention the expansion of forests, deep or crusted snow, cold winters and volcanic ash. Narratives from Alaska suggest that hunting by humans acted in combination with other environmental factors to cause the disappearance of wood bison, and that the less forested nature of the terrain during the late Holocene made bison especially vulnerable to hunters.

The hunting technology and strategies described in Athabascan oral accounts are consistent with existing knowledge of big game hunting techniques used by early Athabascan hunters. However, the reported use of dogs as an aid in hunting bison warrants discussion. Dogs were widely used by the *Gwich'in* to hunt moose and caribou, assisting hunters on snowshoes, especially in late winter when snow was crusted, and to pursue wounded animals (Osgood 1936; McKennan 1965; Nelson 1973).

Behavioral studies of interactions between wolves (*Canis lupus*) and wood bison indicate that dogs may have been effective in holding bison in a given area, and diverting their attention while hunters approached. Carbyn et al. (1993:178-210) describe hunting strategies of wolves in Wood Buffalo National Park, Canada, noting that bison herds often remain stationary for extended periods in the presence of wolves, relying on joint defensive behavior rather than flight. Wolves may spend hours or days in proximity to bison herds before causing a stampede and attempting a kill, or isolating a vulnerable individual. Bison often travel considerable distances after being stampeded by wolves. These researchers also found that a careful and patient approach allowed human observers to follow and observe wood bison at close range, with little disturbance to the animals. The behavioral response of bison to domestic dogs may be much the same as their response to wolves.

Radiocarbon dates for relatively recent bison specimens from Alaska, Yukon and NT range from 170 to 11,900 years before present (Table 1). A few additional specimens from this region have been taxonomically referred to *B.b. athabascae*, but are not yet dated. In combination with archaeological and paleontological data, the oral narratives suggest that bison also occurred along the western arctic coast of Canada during the Holocene, where they likely coexisted with caribou and muskoxen (McGhee 1996:85-93). Archaeological evidence representing early (Cinq-Mars 1991) and late (Harington 1990; Morrison 1997) Holocene sites, as well as oral accounts, indicate humans in this region hunted bison. The distribution of wood bison remains and other historic information suggest that Holocene bison populations were most prevalent in interior Alaska and in northwestern Canada (Figure 3). If the late Holocene climate was similar to the present, the distribution of late Holocene bison remains may reflect relatively low snow accumulation, and less icing and wind-packed snow in this region than in areas to the west (National Oceanic and Atmospheric Administration 1986).

The distribution of late Pleistocene fauna was strongly affected by changes in the Cordilleran and Laurentide ice sheets, which covered much of western Canada and southern Alaska during this period (cf. Matthews 1982; Pielou 1991). Radiocarbon dates for late Pleistocene bison in western Canada (Figure 4) were obtained from localities in west central Yukon which, along with interior Alaska, remained largely ice-free during this period. The apparent hiatus in radiocarbon dates between about 20,000 and 13,000 BP for bison in northwestern Canada may reflect glacial advances and associated changes in environmental conditions which occurred between about 24,000 and 17,000 BP (Hollin and Schilling 1981; Dyke and Prest 1987). The subsequent glacial recession and concomitant expansion of bison populations eastward is reflected in the increased number and wider distribution of dated bison remains between about 13,000 BP and the late Holocene (Figures 3 and 4, Table 1). Bison also colonized south central Alaska after the last major glacial recession, although there is currently only one specimen recorded in this region. The available data suggest that bison colonized new habitat as glaciers retreated, reaching areas as far east as Victoria Island and southern NT during the early Holocene (Figure 3). In contrast, paleontological and zooarchaeological data indicate that bison inhabited the ice-free refugia in interior Alaska continuously during the 48,000-year period represented in Figure 4.

A number of authors have already suggested that bison persisted in Alaska into the late Holocene, and were an important resource for humans during this period (Skinner and Kaisen 1947; Jennings 1968; Harington 1977; Holmes and Bacon 1982; Peek et al. 1987; Guthrie, 1990:286). Holmes and Bacon (1982), and West (1982) suggest that increasingly limited habitat and deep snow, combined with

hunting by "Beringian hunters" likely caused the extirpation of bison. The reasons for the late Holocene disappearance of wood bison in Alaska, Yukon, and parts of Northwest Territories and British Columbia will likely never be understood in the detail that would accompany a similar event in contemporary times. However, published literature and historic accounts suggest a combination of factors that must be considered in explaining the decline and disappearance of wood bison, including predation by wolves and bears, hunting by humans, environmental factors that altered the amount and distribution of suitable habitat, and meteorological or climatic factors.

Predation

Studies of extant northern bison herds suggest it is unlikely that predation by wolves or bears, alone or in combination, would have led to the extirpation of healthy wood bison herds. Introduced or reintroduced herds at several locations in Alaska and northern Canada have achieved, and maintain, viable population levels without significant predator control. Mortality from predation is rare in most herds, even where wolves, black bears (*Ursus americanus*) and grizzly bears are common. Several northern bison herds are limited primarily by regulated hunting, with predation being only a secondary cause of mortality (Gates and Larter 1990; DuBois and Stephenson 1998; Whitman and Stephenson 1998; B. Hayes, pers. comm.). However, other bison populations recently infected with cattle diseases (bovine tuberculosis and brucellosis) may be more susceptible to the demographically limiting effects of predation (Joly et al. 1998).

Several studies have applied metapopulation modeling and knowledge of island biogeography, habitat fragmentation, and population ecology to the question of large mammal extinction (Armbruster and Lande 1993; Beck 1996; Ward 1997). These studies show that even modest levels of exploitation by predators, including humans, have substantial effects on the survival of isolated large mammal populations. Various studies show that isolated populations of birds and mammals are more vulnerable to extinction than larger, contiguous populations (MacArthur and Wilson 1967; Brown 1978; 1986: Grayson 1991). Lande (1988) emphasized the importance of stochastic demographic factors and habitat distribution in determining extinction threshholds for wildlife populations.

It has been suggested that hunting by humans affected the distribution and abundance of a number of large mammal species in North America during the late Pleistocene and Holocene (cf. Martin and Klein 1984; Martin and Wright 1989; McGhee 1996:85: Ward 1997; Whitney-Smith 1998; Martin and Szuter 1999). In this model the high return per unit effort in hunting large mammals resulted in their being preferred prey for early humans (Winterhalder 1981a, 1981b; Feit 1987; Smith 1983; Stephens and Krebs 1986), while the ability of humans to rely on alternative resources such as fish, small game and plants mitigated the adverse consequences of overexploitation of large ungulates (Kay 1997; 1998). The effectiveness of aboriginal hunting techniques allowed hunters to kill prime-age animals in addition to more vulnerable individuals, and to select for female ungulates under certain conditions (Kay 1994a, 1995, 1997, 1998; Stiner 1990).

There is some evidence that aboriginal hunting in Alaska resulted in declines or local extirpation of some species including Dall sheep, muskox, moose and brown bears during the late Holocene (Campbell 1978; Lent 1998; LeResche et al. 1974; Coady 1980; Birkedal 1993). Similarly, unregulated hunting by aboriginal people appears to have been an important factor in the decline or disappearance of muskoxen in parts of Canada (Stefansson 1921; Hone 1934; Harington 1961; Tener 1965; Gunn et al. 1984; Will 1984). Lent (1998) suggests that hunting could have led to the disappearance of muskoxen in Alaska even though they were not a staple resource for most indigenous people. Three Athabascan elders who contributed to our study suggest that hunting played a role in the disappearance of wood bison in Alaska, citing the relative ease with which bison were hunted and killed, periodically high human populations, and the need to hunt intensively during periods when food was scarce. Other historical accounts from northeastern Alaska and the Yukon Flats also suggest that human populations sometimes affected the abundance of big game in the region. The *Gwich'in* stories of Johnny and Sarah Frank of Venetie (Mishler, 1995: 11-13) describe how in the early days "...there were hardly any big game animals because there were too many people." These accounts refer to fluctuations in human populations in this region, and describe how "...when big game animals were scarce, lots of people froze to death." References to famines are common in the legendary history of the Chandalar and Tranjik *Gwich'in* (McKennan 1965; Nelson 1973).

The value of bison as a resource and their vulnerability to the hunting implements and techniques of early humans (West 1982) may have resulted in hunting being an additive mortality factor which, in combination with predation and other sources of mortality, affected the population dynamics of bison. The apparent scarcity of moose in much of Alaska during the late Holocene (Yesner 1989; LeResche et al. 1974; Coady 1980) may have accentuated the importance of bison as a big game resource, as would the seasonal or annual scarcity of caribou in many areas (Burch 1972). The behavioral characteristics of female and juvenile bison, which occur almost exclusively in herds (Komers et al. 1993), would increase their vulnerability (Lande 1988) and the likelihood that more than one animal would be taken in an encounter with human hunters (Fisher and Roll 1997). The possibility that changes in hunting technology improved the effectiveness of hunters should also be considered. The development of archery or other improvements in technology during the late Holocene (Blitz 1988) may have altered the relationship between hunter effort and return.

Habitat Availability

Guthrie (1982:314) indicates that in contrast to some other species represented in Pleistocene megafauna such as horses (*Equus sp.*) or proboscideans, bison are able to cope with relatively deep snow. Some earlier studies suggest that windswept areas adjacent to mountainous terrain were the

most important habitat for Holocene bison in Alaska, based on the premise that bison are not well adapted to substantial snow accumulation (cf. Ager 1974; Holmes and Bacon 1982). However, the distribution of wood bison remains (Figure 3) and geographic referents in oral accounts indicate the presence of late Holocene bison in low elevation habitat. Current evidence suggests that such areas were an important habitat for wood bison in Alaska and Yukon. Despite indications that meadow habitat declined during the late Holocene, recent studies show that the Yukon Flats and other parts of interior Alaska continue to offer suitable habitat for bison herds at or above the level currently estimated to represent a minimum viable population (Newmark 1987; Berger et al. 1995; Dubois and Stephenson 1998; Whitman and Stephenson 1998; ADF&G unpublished data; Wood Bison Recovery Team 1998). The quantity and quality of potential bison habitat in Alaska is substantially greater than in Yukon (Reynolds et al. 1982b; M. Hoefs, pers. comm.), and rivals or exceeds that found in wood bison range in other parts of Canada (Berger et al. 1995; Gates 1992, H. Reynolds, pers. comm.).

Extant wood bison populations occur primarily in low elevation habitat where sub-hygric meadow systems are intermixed with boreal forest (Larter and Gates 1991), further suggesting that Holocene bison were not restricted to windswept habitats. Bison are adapted to temperatures of -48 F or lower (Fuller 1962; Peters and Slen 1964; Christopherson et al. 1978), and prosper in areas where snow depths average 24-30 inches or more (Larter and Gates 1991; Carbyn et al. 1993). Meagher (1973, 1976) concluded that bison can tolerate deeper snow than other northern ungulates, based on the fact that plains bison have prospered in Yellowstone National Park despite a harsh winter climate, foraging in snow depths exceeding 50 inches. However, snow depth and hardness influence bison foraging behavior, as demonstrated by Meagher (1976), who found that snow depth had a major influence on habitat selection in Yellowstone Park. Wind-packed or ice crusted snow also presents difficulties for bison, and snow density was the principle factor influencing the selection of feeding sites by wood bison in the Slave River lowlands (Reynolds and Peden 1987).

There are a number of references to historic changes in vegetation in interior Alaska and other northern regions, with a trend toward expansion of shrubs and forests during the last few centuries (Vanstone 1974; McKennan 1965); a variety of biotic and abiotic factors appear to be involved (cf. Jacoby, and D'Arrigo. 1989; Campbell et al. 1994; Zimov et al. 1995; Chowns et al. 1998; Overpeck et al. 1997). Several elders from communities on the Yukon Flats also referred to oral traditions indicating the area was formerly more open, with fewer trees and shrubs and more extensive meadow systems (O'Brien 1997:37).

At present the Yukon Flats is characterized by a diverse mosaic of mixed spruce-poplar and spruce hardwood forests, spruce muskeg, and successional and climax stands of willow and alder. Both wet and dry meadows are common, comprising approximately 12 percent of the total area. Despite the apparent reduction in the amount of available meadow habitat, the Yukon Flats and parts of the Tanana Valley continue to offer suitable habitat for viable bison populations (Berger et al. 1995; ADF&G unpublished data).

Bison are eclectic, with an ability to exist in a variety of climatic and habitat regimes ranging from subarctic boreal and eastern deciduous forest, to relatively arid conditions in the southwestern United States (van Zyll de Jong 1986, Dary 1989). In recent decades wood bison have been reintroduced in the southern Yukon, and plains bison have been introduced in the Delta, Farewell, Copper River and Chitina River areas in Alaska. Except for the Copper and Chitina River herds, which settled in poor quality habitat (Miquelle 1985), these herds increased at high rates and continue to show high productivity (DuBois and Stephenson 1998; Whitman and Stephenson 1998).

It is clear that suitable bison habitat is still available in parts of the range once inhabited by wood bison, a fact that opposes the idea that changes in habitat caused their decline and disappearance. Further, the nature of recent environmental changes that are reported to have occurred in interior Alaska indicate that wood bison declined and disappeared at a time when the extent of meadow habitat was greater than at present. Lent (1998) observed that the successful reintroduction of muskoxen to northern Alaska demonstrates that suitable habitat for this once extirpated species continues to exist. However, changes in the distribution of suitable habitat, in combination with hunting and other mortality factors, probably contributed indirectly to the disappearance of wood bison in Alaska.

Rather than being more widely distributed over the landscape, as was the case during the Pleistocene, Holocene bison habitat became more limited through time (Guthrie 1990), although it was not eliminated as has sometimes been suggested (Guthrie 1982). The transition from relatively treeless steppe to increasingly forested terrain during the late Pleistocene and Holocene would have gradually created a mosaic in which bison habitat was largely confined to low-lying areas with upland or riparian meadow habitat. This would have included the Yukon and Tanana lowlands in Alaska, and/or windswept habitats adjacent to large mountain valleys (Holmes and Bacon 1982; Guthrie 1990). This is the general pattern of distribution suggested by the occurrence of skeletal remains of Holocene bison (Table 1; Fig. 3). However, more widespread sedimentation and greater human activity at low elevations would probably increase bone preservation and enhance the likelihood of discovery, making it difficult to assess the degree to which uplands might have been used by late Holocene bison.

Habitat for late Holocene bison populations most likely occurred in discrete patches that, while capable of supporting viable populations, were nonetheless separated geographically. Once a subpopulation was extirpated, geographical constraints and stochastic events affecting founding populations would limit the likelihood of recolonization. This is consistent with the behavior of existing northern bison populations, with distribution being substantially limited by geographic barriers such as mountains or extensive stands of unbroken forest (Gates and

Larter 1990; Larter and Gates 1991). The seasonal and annual movements of extant northern bison populations are largely constrained by the distribution of habitat (Larter and Gates 1990). The distribution of late Holocene bison was probably limited in comparison to moose, caribou and sheep, which persist through the present.

Lent (1998) concludes that small numbers of muskoxen persisted in the eastern Brooks Range, after their extirpation in northwestern Alaska in the mid 1800s, in part because of the relatively low human population density in the mountainous terrain in the area. Historic accounts, including those presented here, indicate that resource availability and other attributes caused areas adjacent to large rivers to be a year-round focus of human habitation during the late Holocene (cf. Schneider 1986; Luke 1998). This pattern of late Holocene human land use would have placed wood bison populations in juxtaposition with human populations, making them accessible to human hunters on a year-round basis, and limiting the occurrence of refugia (Taylor 1984) where bison were not subject to human exploitation. This situation contrasts with that on the Great Plains, where migration reduced the vulnerability of plains bison to predation (Kay 1994a; 1996).

Influence of Climate

Limitations in the current understanding of the late Holocene climatic regime make it difficult to draw precise inferences regarding the influence of climate on the geographic distribution of wood bison in the northwestern part of their original range. Nevertheless, it is difficult to account for the disappearance of wood bison from Alaska and northwestern Canada on the basis of environmental or climatic changes alone, unless there were catastrophic weather events on a regional scale, or broad, uniform and sustained changes that led to the elimination of suitable habitat. There is currently no evidence for either of these phenomena.

The boreal forest is the product of frequent and often pronounced climatic fluctuations since its establishment following the most recent glacial period (Juday et al. 1998). During the last glacial period the arid climate in lowland central Alaska, central Yukon and eastern Russia precluded the formation of ice sheets, and cool and arid conditions prevented the expansion of forests. Following the end of full glacial conditions and a warming trend beginning about 14,000 years ago, forests expanded northward (Pielou 1991). In addition to climatic and vegetational changes that have occurred on a scale of millennia, decadal and century long climatic changes altered plant species abundance and distribution (Bartlein 1988).

Based on studies of Greenland ice cores, tree-rings and other paleoecological proxies, Holocene climate was characterized by significant diversity, with environmental change occurring on an increasingly regional basis. Continuous paleoclimatic records from the GISP2 ice core show variability on an annual to millennial scale, indicating that Holocene climate was significantly more complex than glacial ice age climate (Greenland Ice Core Project 1993; O'Brien et al. 1995; Overpeck et al. 1997; Ice Core Working Group 1998). The Holocene climate was also comparatively stable over variable periods of time (Guthrie 1990). Some oral accounts (see above) mention periods of deeper snow or extreme cold in the past (see also Fleener 1998), although these are difficult to reconcile with Little Ice Age (LIA) models at this point.

There is general agreement that glaciers and arctic sea ice expanded globally at various times during the Little Ice Age (LIA), which is generally viewed as occurring from the 13th through the 19th centuries (Grove 1988). Overpeck et al. (1997) review evidence for climatic and environmental change in the Arctic during the last four centuries, based on a variety of paleoenvironmental indicators. Their study reveals large-scale variability over the past 400 years, but suggests that declines in summer insolation and other factors led to successively cooler summers, culminating in the Little Ice Age. The onset of the LIA occurred about A.D. 1400 following several centuries of warming during the so-called Medieval Warm Period (MWP). Cold, dry conditions and increased atmospheric circulation generally characterized the LIA. Similar conditions appear to have prevailed at various times during the Holocene (Kreutz et al. 1997). Although patterns related to the LIA were global in nature, the period is not defined by uniform cooling on a regional scale. There is no unambiguous and uniform LIA signal recorded in tree-rings (Jacoby and D'Arrigo 1989; D'Arrigo and Jacoby 1992). Instead, the period includes both warm and cold anomalies that varied geographically and may have persisted into the 20th century.

Increases in the severity of winter storms and extent of sea ice during the LIA were accompanied by changes in agricultural production which contrasted with milder conditions during the Medieval Warm Period (Lamb 1995). The GISP2 paleo-atmospheric record indicates the LIA had the most abrupt onset of any of the rapid Holocene climate change events (O'Brien et al. 1995), and involved the most dramatic change in atmospheric circulation and surface conditions in the last 4000 years, with similar timing and magnitude in both polar hemispheres. Summer temperatures from A.D. 1597 to 1730 in both hemispheres were the lowest in the last 500 years (Kreutz et al. 1997). However, the LIA was one of the shortest cold intervals during the last 110,000 years, and was substantially shorter than other major climatic changes during the Holocene. No single factor appears to be responsible for bipolar changes during the LIA. Moreover, there is no indication of a general increase in volcanic activity during the last 600 years (Kreutz et al. 1997), although a steady warming trend from 1840 to the mid 1940s may have been precipitated, in part, by frequent, sulfur-producing volcanic eruptions (Overpeck et al. 1997).

Studies of past climates based on tree-rings reveal a pattern of temperature variation in interior and northern Alaska from the 1500s to the present. This record is in general agreement with overall trends at high latitudes in the Northern Hemisphere. Temperatures in interior Alaska were distinctly cooler during the LIA than during the 20th century, and reconstruction from tree-rings shows the effects were most pronounced in the early part of the record (from at least the 1500s to 1700). This was followed by a partial warming in

the early 1700s, an abrupt return to colder conditions from about 1800 to 1840, and a steady warming from 1840 to the mid 1940s (Jacoby and D'Arrigo 1989; D'Arrigo and Jacoby 1992; Overpeck et al. 1997). This pattern is apparent in tree-ring data obtained at several sites in northern Alaska and northwestern Canada (Overpeck et al. 1997).

Warmer winters may have been correlated with heavier snowfall, rendering bison more vulnerable to human hunters and other predators, or with windy or icing conditions that redistribute and harden snow and thus interfere with the foraging ability of bison. Russell (1898) reports that exceptionally deep or ice-crusted snow during a single winter (apparently the winter of 1870) decimated wood bison populations in the Slave River area. Similarly, Harington and Cinq-Mars (1995) suggest that sudden winter thaws may have affected the survival of saiga antelope (*Saiga tatarica*) and other megafauna during the late Pleistocene in northwestern North America.

Murray (1910) notes that moose were fairly common in the Fort Yukon area in 1847-48, while oral narratives (McKennan 1965; this study) indicate they were scarce in earlier times. Murray's observations pertain to a period immediately following the most extended period of increased weather severity in the LIA, and suggest moose had increased in numbers and distribution following the period of absence or extreme scarcity described in historical accounts. It is unlikely that bison populations would have been decimated at the same time that moose populations expanded, considering that bison are relatively well adapted to deep snow and cold (Peters and Slen 1964; Christopherson et al. 1978, 1979; Larter and Gates 1991; Carbyn et al. 1993; Meagher 1973, 1976). Similarly, Lent (1998) concludes there is no clear evidence that climatic change during the late Holocene caused the extinction of Alaskan muskoxen, noting that larger fluctuations in climate had occurred previously (Haworth 1989). Kay (1997: 145-146) concludes that the LIA or other climatic or weather events do not account for the general scarcity of moose prior to the very late Holocene in much of North America.

Bison persisted in Alaska and northwestern Canada for at least several hundred thousand years despite climatic fluctuations that were frequent, dramatic and abrupt in comparison to the relatively benign climatic regime during the Holocene (Guthrie 1990). This suggests that the temporally limited and modest climatic changes during the LIA are an unlikely cause for the demise of wood bison. The LIA did not result in the extirpation of other large ungulates in the region including moose, caribou or Dall sheep. These species can be strongly affected by severe winter weather and snow conditions (Fancy and White 1985, 1987; Heimer et al. 1994; Adams and Dale 1998), with snow depth being particularly important in affecting the population dynamics of moose (Kelsall 1969; Peterson and Allen 1974; Gasaway et al. 1992).

Current Knowledge of Wood Bison Biogeography during the Late Holocene

The results of our study support earlier indications that bison persisted during much of the Holocene in Alaska (Holmes and Bacon 1982; Guthrie 1990), and that substantial populations persisted in some areas longer than was previously thought. The available skeletal remains of wood bison, associated radiocarbon dates, and oral and written narratives establish that: 1) bison were widely distributed on the late Holocene landscape, and that wood bison populations persisted in northern and eastern Alaska and adjacent Canada until their extirpation during the last few hundred years; 2) bison were a resource of some importance for Athabascan and other Native peoples during the late Holocene; 3) bison populations were high enough to persist over a period of several thousand years and to support significant human use; and 4) low elevation meadow systems, windswept areas at higher elevation, and some areas that are presently arctic tundra supported late Holocene bison populations.

Based on written accounts by Europeans who traveled in northwestern Canada during the late 18th and early 19th centuries (Gates et al. 1992), as well as oral accounts and skeletal remains, van Zyll de Jong (1986) indicated that the so-called "historic" range for wood bison included northern Alberta, the southwestern NT, and parts of northern British Columbia and Saskatchewan (Figure 3). Skinner and Kaisen (1947) had earlier suggested that wood bison were found in the eastern Rocky Mountains as far south as New Mexico. However, subsequent craniometric analyses indicate the southern limit of wood bison distribution was some distance north of the US-Canada border, and that specimens from areas west of the Great Plains in the United States represent *B.b. bison* (van Zyll de Jong 1986).

The recent distribution of bison in southern Canada, where wood and plains bison populations might have overlapped, was particularly germane to van Zyll de Jong's study of the taxonomic status of recent bison. Based on data from three subfossils in Alaska and four from Yukon and northern British Columbia, van Zyll de Jong (1986) further suggested that the "prehistoric" range of wood bison extended "...north and west into the Yukon and Alaska." In consultation with van Zyll de Jong, Canada's National Recovery Team for Wood Bison subsequently revised the boundaries for the original range of wood bison to include additional parts of northern Alaska and Canada (C.C. Gates, pers comm. 1998), based on additional subfossil evidence (Harington 1990). This region included interior, arctic and western Alaska and part of northwestern arctic Canada, encompassing parts of the north that were also classified as original range by Skinner and Kaisen (1947).

Based on existing historical documentation, we describe three general categories relative to Holocene bison distribution in northern North America (Figure 3). The region that appears to have been inhabited by small horned *B. bison* (*sensu* Wilson 1978; 1996) at some time during the Holocene is shown. This region includes areas previously referred to as "prehistoric" and "historic" range for wood bison (van Zyll de Jong 1986), as well as an additional part of the arctic coastal region in Canada where recent paleontological data reveals their presence during the early Holocene. The known distribution of wood bison during the